CANOPY DYNAMICS OF TREES AND SHRUBS WITH PARTICULAR REFERENCE TO ARID-ZONE TOPFEED SPECIES

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SUMMARY

A study is reported in which foliage gain and loss was followed in canopies of tree and shrub populations. Data are presented tracing concurrently quantities and rates of leaf gains and losses in stands of five arid-zone topfeed species in stands at Yudnapinna, South Australia, during the period May 1965 to January 1967. These data are examined also with reference to time of year and rainfalls which occurred during the period.

The performances of the five species are grouped into three categories characterized with respect to various features such as number of phases, synchronization of foliation and defoliation, and seasonal periodicity. The significance of both method and results in revealing canopy dynamics in arid regions is discussed.

INTRODUCTION

Topfeed or browse species are those trees and shrubs in rangeland vegetation which produce stock fodder. Some of this foliage is directly accessible to stock, some is shed to the ground. Mulga (*Acacia aneura* F.v.M.), bullock-bush (*Heterodendrum oleaefolium* Desf.) and plum-bush (*Santalum lanceolatum* R.Br.) are typical Australian examples.

The pastoral importance of topfeeds is recognized and has been extensively discussed; for example, in Joint Publication 10 of the Imperial Agricultural Bureaux it was pointed out that "probably more animals feed on shrubs and trees, or on associations in which shrubs and trees play an important part, than on true grass or grass-legume pastures, short and tall-grass ranges, and steppes". Topfeeds certainly have importance in the Australian arid-zone.

With few exceptions, published data about canopy growth and hence fodder production by topfeed stands in the Australian arid-zone are lacking.

Principles for determining productivity of tree stands are well established (Ovington, 1962). Methods refer mostly to forest and agricultural situations where sites, climates and stands are closely specified, cyclic and predictable, and emphasize mean production of timber by weight or volume, or total yield by weight or calorific equivalent. In the Australian arid zone, stands are not closely specifiable because their biology is not well understood, and climate is neither cyclic nor predictable in many important respects. Further, emphasis regarding topfeeds is on foliage alone, and preconceptions, like prior literature on these topfeeds, are absent. It is necessary to adopt an approach consistent with this context. Such an approach, implemented in this study, has yielded relevant data about production rates of arid-zone topfeed species, and this paper reports and discusses the approach itself and results obtained by its use.

METHODS

For each species the study unit was the accessible outer foliage of the natural stand, regarded as a population of shoots. This population was sampled by

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restricted randomization, that is, the total stand was first sectored and then random samples were drawn pro rata from each sector. A tag was affixed on each sampled shoot axis between the sixth and seventh leaf or leaf-bearing position proximal to the apex. Between 100-150 samples were tagged per stand. Total leaf number distal to tags was regarded as initial capital or quantity, susceptible to gain and loss. Records were kept of leaves and leaf-bearing positions on individual shoots; changes in leaf numbers were thus observed and recorded at intervals during a protracted period. The use of tags for this purpose is well known (Nelson 1930, Njoku 1963).

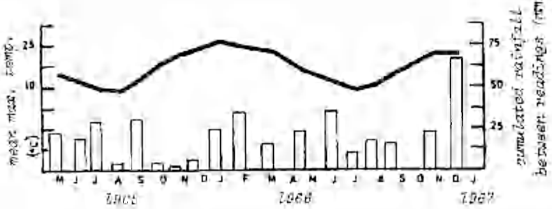


Fig. 1. Shows mean maximum daily temperature (°C) and accumulated rainfalls (mm) for successive periods.

Experimental sites were located on Yudnapinna Station (an arid-zone pastoral lease in South Australia) at lat. 32.2°S, long. 137.5°E, in vegetation described by Jackson (1958), who also described associated climate, physiography and soils. Climatic data for the period were obtained from the Yudnapinna records of the Commonwealth Bureau of Meteorology. The species studied were *Acacia sowdenii* Maiden, *Myoporum platycarpum* R. Br., *Heterodendrum oleaefolium* Desf., *Cassia nemophila* var. *coriacea* (Benth.) Symon and *Cassia nemophila* var. *platypoda* (R. Br.) Benth. Voucher specimens are deposited in the State Herbarium of South Australia.

RESULTS

Summarized data are presented in figures 2 and 3. Figure 2 shows the course of cumulative leaf gain, cumulative loss, and cumulative gain/loss balance for each of the five species; Figure 3 shows rates of gain and loss for each of the five species. Figure 1 shows graphs of mean maximum daily temperature, and accumulated rainfalls for successive periods, in the study area.

The five species fall into three categories on differences and similarities of performance.

Category I

A. The *Heterodendrum oleaefolium* stand (Figs. 2d; 3a).

Observations began in April 1965. No changes occurred until August, after mean temperatures rose from their winter low. Foliation and defoliation then occurred at more or less equivalent low rates until November, after which rates increased until February 1966. Net gain within samples was then about 25%. With the passing of peak summer temperatures, foliation rates fell to near zero by September, as did defoliation rates. From February to October 1966 net foliage declined by about 20%. Again when temperatures began to rise in summer, rates of foliation and defoliation increased until December and began to decline by January 1967. Net gain to initial capital was about 75% when observations ended.

The following points are established:

(a) This stand exhibited canopy dynamics which appear to be cyclic on a seasonal basis. (In this locality rainfall is not seasonal hence "season" implies only temperature and photoperiod cycles.)

(b) The characteristics of these canopy dynamics were (i) rates which increased rapidly in spring from near zero, sustained high values until thermal midsummer, then declined gradually to very low rates by thermal midwinter; (ii) synchronous and similar rate changes in foliation and defoliation; (iii) the differences in the magnitude of these rates caused net increases in the period November to February, with little change or slight decline over intervening periods.

(c) Foliation and defoliation rates changed irrespective of rainfalls, and showed no direct response to rainfalls.

B. The *Acacia sowdenii* stand (Figs. 2b; 3b).

The performance in this stand was generally similar to that in the *Heterodendrum oleaefolium* stand regarding cyclic rate changes, no obvious reaction to rainfalls, and net losses during winter. There are however differences in particulars, namely (i) curve inflexions occurred later in summer, (ii) foliation and defoliation rate changes were not well synchronized, and (iii) a higher net gain was attained over the period.

Category II

The *Myoporum platycarpum* stand (Figs. 2c; 3c).

This performance, like those in category I, showed no direct reaction to rainfalls, but differed in that higher rates of foliation were sustained longer and rate changes were gradual rather than sharp. Net gains were sustained during the entire period, and ultimate net gains were considerably higher than in Category I. Since all curve inflexions were relatively suppressed, so was expression of foliation/defoliation synchronization, and apparent seasonal cycle.

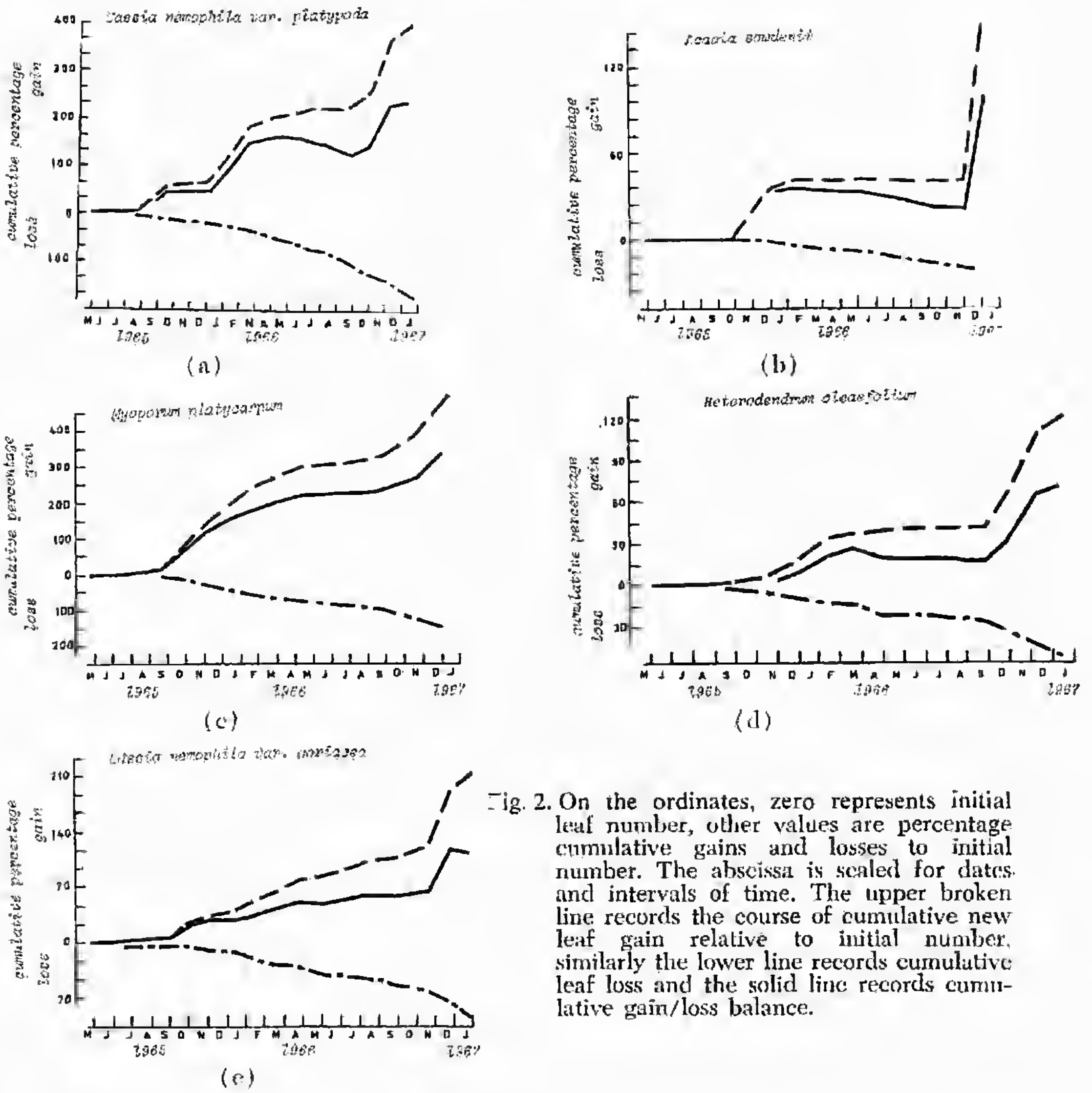
Category III

A. The *Cassia nemophila* var. *platypoda* stand (Figs. 2a; 3d).

This performance differed markedly from those of other categories in that three phases of rate-change occurred during the period where other performances exhibited only two. Rainfalls were the only non-seasonal environmental variables measured; there was no obvious relationship between the timing of these and the midle phase of rate-change. Substantial nett loss occurred between the last two phases of rate-change. There was no close relationship between rates of foliation and defoliation. Overall net gain was comparable wtih Category II.

B. The *Cassia nemophila* var. *coriacea* stand (Figs. 2e; 3e).

This performance was essentially similar to that of *Cassia nemophila* var. *platypoda*, viz.: three phases of rate change instead of two. Net loss was sustained between the first two of these; overall net gain was lower.



(a)

(b)

(c)

(d)

(e)

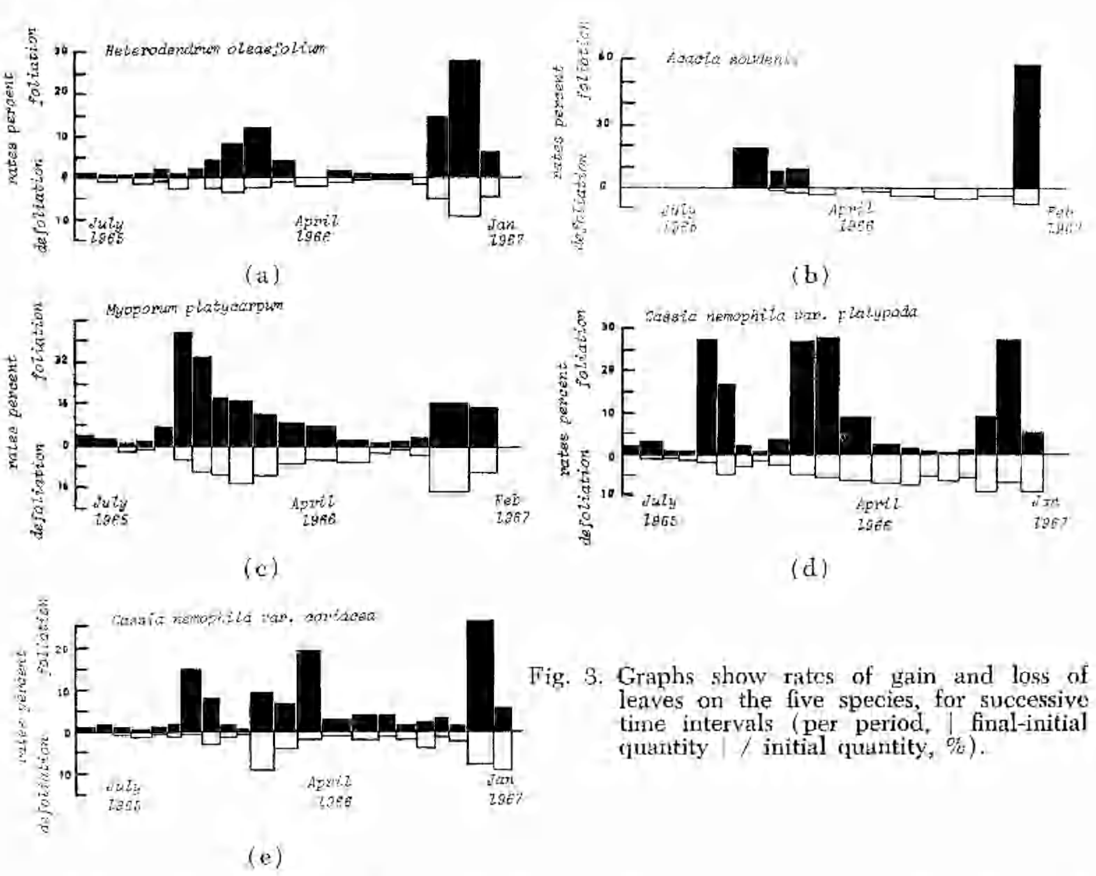
Fig. 2. On the ordinates, zero represents initial leaf number, other values are percentage cumulative gains and losses to initial number. The abscissa is scaled for dates and intervals of time. The upper broken line records the course of cumulative new leaf gain relative to initial number, similarly the lower line records cumulative leaf loss and the solid line records cumulative gain/loss balance.

DISCUSSION

The first noteworthy feature is that of apparent seasonal regularity in the way some species gain and shed leaf. There are two aspects to this, first, rainfall (8 in. annual average in the area) is erratic and, apart from slight elevation about February, monthly averages over 30 years are about equal; second, apparent cycles of growth coincide with the build up and climax of high summer temperatures and related water-stress. This situation parallels that in Dark Island Heath (Specht 1957), where main growth is in summer at times of soil water depletion. As opposed to such heath, these Yudnapinna stands are not even guaranteed a predictable wet winter. Such growth phenomena remain unexplained.

The second important feature is variation in performance between stands. If eventual consideration be given to the informed use of arid-zone topfeeds, attention must be directed then to the implications of this variation. Thus the timing of Category I production phases appeared to be predictable from a knowledge of date alone, and independent of the timing of particular rainfalls. This predictability attached, in *Heterodendrum oleaefolium* for example, to both fresh leaf production and litter drop. Category III stands, in contrast, represented a different kind of topfeed, since they displayed three phases of activity versus two for other species in their immediate vicinity. The Category II species represented yet another type, where leaf gain proceeded in a relatively even fashion while activity in other stands either accelerated or declined. There is certainly no suggestion that Yudnapinna topfeed stands all behave alike.

Most Yudnapinna stands exhibited periods of activity not related to particular rainfalls despite the arid habitat, which offsets any idea that "likely effectivenesss" of precipitations (Beard 1968) is necessarily a first issue in the performance of arid-zone plants.



(a) (b)

(c) (d)

(e)

Fig. 3. Graphs show rates of gain and loss of leaves on the five species, for successive time intervals (per period, | final-initial quantity | / initial quantity, %).

Figures 2 and 3 show that topfeed canopy dynamics are revealed simply and clearly by tagging; a further step might be to relate sampled population to total stand canopy. This would be difficult; it is much more complex to document the course of events on every branch in the canopy, with respect to every leaf and bud it bears between its apex and most proximal leaf. The oldest leaves furthest from the shoot tip are more likely to fall than the tip leaves; taken into account, this would reduce percentage net gains to different, lower figures. Similarly, top canopy shoots and inner canopy shoots perform differently to each other and to accessible shoots. Eventually, consideration of limb and whole plant input and death might be necessary. In practical terms, learning the added information might not justify the effort. Recourse to other techniques such as litter-trapping (Bray and Gorham 1964) might be explored first, since the question of what information is desirable must be balanced against the cost of obtaining it. No available method, however, appears superior to counting leaves on tagged shoots possibly combined with measurements of shoot length for following canopy dynamics, where the purpose is the interpretation of arid zone stands as rangeland fodder components.

Ultimately, best advances may be made by considering stand production as of an assemblage of specified individuals studied separately. At present information is lacking whereby stand composition may usefully be specified; the typical Australian topfeed stand is an unknown entity regarding internal age and stage relationships, although data are accumulating.

Synchronization of foliation and defoliation in *Heterodendrum oleaefolium* prompts ideas that this synchronization holds for individual trees, that internal nutrient cycling could be involved, and that interesting physiological mechanisms will be found responsible. Further attention to this must await investigations of individuals, not of the stand as a whole.

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REFERENCES

BEARD, J. S., 1968. Drought effects in the Gibson Desert. J. Roy. Soc. W.A. **51**, pp. 39-50.

BRAY, J. R., and GORHAM, E., 1964. Litter production in forests of the world. Adv. in Ecol. Res. **2**, pp. 101-157.

JACKSON, E. A., 1958. Soils and hydrology of Yudnapinna Station, S.A. C.S.I.R.O. Soil and Land Use Series No. 24.

JOINT AUTHORS, 1947. The use and misuse of shrubs and trees as fodder. Imp. Agric. Bureaux Joint Publication No. 10.

NELSON, E. W., 1930. Methods of studying shrub plant in relation to grazing. Ecol **2**, pp. 764-769.

NJOKU, E., 1963. Seasonal periodicity in the growth and development of some forest trees in Nigeria. J. Ecol. **51**, pp. 617-624.

OVINGTON, J. D., 1962. Quantitative ecology and the woodland ecosystem concept. Adv. in Ecol. Res. **1**, pp. 103-192.

SPECHT, R. L., 1957. Dark Island Heath (Ninety-mile plain, South Australia). V. The water relationships in heath vegetation and pastures on the Makin Sand. Aust. J. Bot. **5**, pp. 151-172.